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Temporal patterns of storage and flux of N and P in young Teak plantations of tropical moist deciduous forest, India

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Abstract: Teak (*Tectona grandis* Linn. f.) ranks among the top five tropical hardwood species and is being promoted for use in plantations in its non-native range due to its high economic value. However, there is a general lack of data on ecosystem functioning of teak plantations. We aimed at understanding storage and flux of nutrients related to young plantations of teak. Cycling of nitrogen (N) and phosphorus (P) in a chronosequence of plantations (1, 5, 11, 18, 24 and 30 years) was studied in the Moist Deciduous Forest Region of North India with the objective of investigating the nutrient cycling pattern at younger age since the current trend of harvesting age of the species in several tropical countries is being drastically reduced for quick return from this high value crop. Standing state, nutrient uptake, nutrient return and nutrient retranslocation in these plantations were estimated by tree harvesting and chemical analysis methods. The range of total standing nutrient across all these plantations was 20.3 to 586.6 kg·ha^{-1} for N and 5.3 to 208.8 kg·ha^{-1} for P. Net uptake of N ranged from 19.4 to 88.9 kg·ha^{-1}·a^{-1} and P from 3.8 to 18.1 kg·ha^{-1}·a^{-1}. Retranslocation of N and P among all the stands ranged from 8.7 to 48.0 kg·ha^{-1}·a^{-1} and 0.01 to 3.5 kg·ha^{-1}·a^{-1}, respectively. Range of total nutrient return was 25.8 to 91.3 kg·ha^{-1}·a^{-1} for N and 2.7 to 10.1 kg·ha^{-1}·a^{-1} for P. N and P use efficiency was between 107.4 and 192.5 g dry organic matter (OM) g^{-1} N, and 551.9 and 841.1 g OM g^{-1} P, respectively. The turnover time ranged from 2.04–13.17 years for N and between 2.40–22.66 years for P. Quantity of N and P in the soil nutrient pool ranged from 2566.8 to 4426.8 kg·ha^{-1} and 372 to 520 kg·ha^{-1}, respectively. Storage and flux of components in different plant parts of different aged plantations were assessed and depicted in compartment models. Percentage storage in soil, litter and vegetation ranged from 82% to 99%, 0.6% to 2.4% and 0.5% to 15% for N, respectively, and from 63% to 98%, 0.5% to 2% and 1% to 35% for P, respectively. This information could be useful in managing external nutrient manipulation to crops of different ages for optimum biomass production or carbon sequestration.

Keywords: nutrient uptake, standing state, return, turnover time, nutrient use efficiency, compartment model, harvest loss, *Tectona grandis*

Introduction

The functioning of most ecosystems is generally influenced by availability of nutrients. This, in turn, depends on their distribution and rate of cycling at the ecosystem level (Chaturvedi and Singh 1987). Nutrient cycling helps plants accumulate resources and allocate them to growth, maintenance, and reproduction (Harper 1977). This process includes nutrient uptake from soil, their distribution in different plant parts (retention or storage), and return through litter fall (Switzer and Nelson 1972; Turner and Lambert 1983; Westmann 1978). Emphasis has been on retranslocation or nutrient retrieval from senescing leaves and other parts (Chapin and Kedrowski 1983; Karmacharya and Singh 1992; Sharma and Pande 1989; Singh and Singh 1991; Vitousek 1984; Lodhiyal and Lodhiyal 2003; Rouhi-Moghaddam et al. 2008).

Accumulation and distribution of nutrients are affected by age, climate and type of tree species (Ovington 1968). Although relationships vary for different forest communities, nutrient uptake is usually directly proportional to net primary productivity (Rodin and Bazilevich 1967). Part of the total nutrient uptake is utilized within the system for building structure and the remainder is returned to the forest floor after retranslocation.

Biochemically active leaves build mass of nutrients in their tissue which often decline to a minimum as a result of senescence-induced retranslocation (Charley and Richards 1983). This internal cycling of nutrients not only conserves nutrients in the biomass but also prevents loss to the plant through litter fall. Nutrient return to the forest floor depends mainly on the quantity of litter fall which is, in turn, controlled by the age and density of the plantation (Singh and Singh 1991). Litter fall represents an essential link in the organic production-decomposition cycle, and

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thus is a fundamental ecosystem process (Meentemyer et al. 1982) for providing the nutrients to soil for their further uptake.

Teak (*Tectona grandis* Linn. f.) is usually a long rotation species, naturally occurring in Southeast Asia. Teak is also raised in timber plantations in several tropical countries that are outside the natural zone of its occurrence. Now, this species ranks among the top five tropical hardwood species (Krishnapillay 2000). The harvesting age of teak has been reduced from 90–120 years to 50 years in traditional forest plantations and further to 15–30 years (Balooni 2000; Pandey and Brown 2000; Tewari 1992) in commercial forestry. There is, however, a general lack of data on ecosystem functioning of teak.

Therefore, we aimed at understanding the following aspects of storage and flux of nutrients related to young plantations of teak: (1) Magnitude of storage of total nitrogen (N) and phosphorus (P); (2) Amount of uptake and internal cycling of nutrients; (3) Quantum of nutrient return through litter fall; (4) Comparison of nutrient cycling aspects in teak with other species and forest types.

Materials and methods

Study site

The present study was done in teak plantations aged 1, 5, 11, 18, 24 and 30 years in the *Tarai* region of *Kumaun* Himalaya. For each age group, three replicate plots were selected. The *Tarai* is a strip of land parallel to the foothills of the Himalayan range and is an outlying belt with deposition of finer materials and abundant soil moisture. Its length extends all along the Himalayan base and its width ranges from 10 to 25 km. The study sites were situated between 29°3′ to 29°12′ N and 79°20′ to 79°23′ E at an elevation range of 230–280 m (Fig. 1).
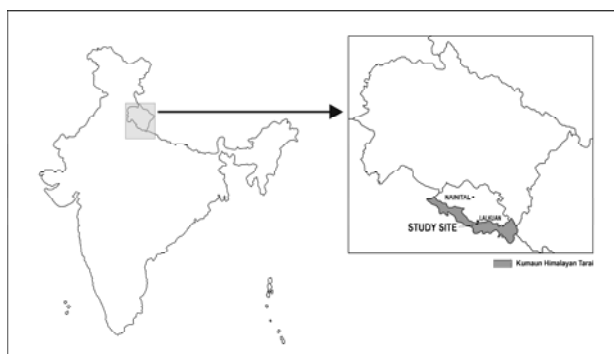

Fig. 1. Study area

Natural vegetation of this area, presently highly altered due to conversion, is "alluvial savannah woodland - type 3/1S1, with some pockets of moist *Tarai* Sal - type 3c/C2c" (Champion and Seth 1968). The low density forest areas were clear felled in the past and were converted into plantations of high yielding species like poplar, eucalyptus, teak and other species.

Climate of this region is subtropical and monsoon type with long dry (eight months) and short wet seasons. Winter extends

from November to mid March. December and January are the coolest months. Summer stretches from mid March to June. June is the hottest month. The rainy season lasts from the later half of June to September. Ten-year (1985−1995) data show that mean monthly temperature ranged from 14.4°C to 31.3°C and annual average rainfall was 1,593 mm. The distribution of average total rain in different seasons is approximately 83%, 3% and 14% in rainy, winter and summer seasons, respectively. Average humidity is 65%. The study area is reported to experience frost events. Soil of this region is a typic hapludoll with a fine loam texture (Kumar and Sharma 1990).

Sample collection

For study of dry matter dynamics we demarcated sample plots, varying from 1.2 to 2.9 ha (1992−1993) in the age series plantations ranging between 15 and 97 ha in area. All the trees were enumerated and grouped into 5 cm diameter class intervals from 0.1−5 cm to 40.1−45 cm. Three representative trees of all diameter classes from all the six plantations (in few cases, however, owing to inadequacy of samples only one tree) were marked and harvested for collection of wood, bark, branch, twig, leaves and roots. Stem, branch and twigs were sorted based on their utility as timber, small wood and fuel, respectively. Roots were excavated by digging pits and root biomass was segregated into stump and lateral root components. Representative samples of different tree components were dried at 90°C until constant weight, mill ground, and powdered using a stainless steel grinder, so that samples could pass a 1 mm mesh. Woody samples were chipped before grinding to facilitate easy grinding.

Chemical analyses

Three replicate samples from the powdered composite samples of different components were subjected to chemical analyses to estimate nutrient concentrations in different parts of the tree. Total N was estimated by microkjeldahl (Jackson 1958) and total P by the phosphomolybdic blue method (Singh and Singh 1991).

Standing state of nutrient

Standing state of nutrient was computed as the sum of the products obtained by multiplying dry weights of tree components by their nutrient concentrations. Standing state in different components was summed to obtain total nutrient storage in the stand.

Nutrient uptake and retranslocation

Nutrient gross uptake was computed by multiplying the values of net primary productivity of different components by their respective nutrient concentrations. Nutrient net uptake was calculated by adjusting for nutrient retranslocation (Singh and Singh 1991). Retranslocation was estimated by Equ. 1 given in

Ralhan and Singh (1987). Using this ratio the amount of re-translocation was calculated.

$$R_N = \frac{m_s - m_a}{m_s} \times 100 \qquad (1)$$

where, R_N is nutrient net uptake, m_s is nutrient mass in leaf at steady state, and m_a is nutrient mass in leaf at abscission.

Nutrient return

We collected litter every month from three litter traps in each age group. Three composite samples of different litter components were analyzed for nutrient concentration. Nutrient return through litter fall was calculated as the sum products of the magnitude of different kinds of litter and their respective nutrient concentrations (Singh and Singh 1991).

Turnover time of nutrient

The turnover time (t) for both the elements in standing vegetation was calculated as the reciprocal of turnover rate (K) i.e., ($t = 1/K$) and turnover rate was calculated by the formula, $K = A/(A+F)$, suggested by Chaturvedi and Singh (1987). Where, A and F are the amount of annual uptake and total standing nutrients, respectively.

Soil nutrient analysis

In each plantation three pits were dug randomly to collect soil samples from 0 to 15, 15 to 30 and 30 to 60 cm depths. The collected soil samples were analyzed for total N and P by kjeldhal and phosphomolybdic blue colorimetric method, respectively (Jackson 1958). The amount of nutrient in soil was determined by multiplying bulk density, soil volume and nutrient concentration values.

Compartment Models

For complete synthesis of a compartment model, certain data from other studies were used since fine root productivity, soil bulk density and complete mineralization of leaf litter were not studied during this investigation. Fine root turnover was calculated from Singh and Singh (1991) as a multiple of eight times that of coarse roots. Our reason for selecting this value was that teak is a deciduous species and their multiple was derived from study of deciduous forest. On the basis of the report of Choompol (1973), fine roots of teak were confined to 30 cm depth, soil volume of this stratum only was taken into account for calculation of nutrient storage in soil. Average bulk density was taken from Lodhiyal (1990) and Bargali (1990), and these studies were conducted in areas adjoining the present study sites. For one year decomposition data in the present study, annual decomposition values were taken from Singh et al. (1993) working in a similar type of forest near our study area.

Statistical analysis

The data were subjected to one way analysis of variance (ANOVA) which indicated no significant difference between replicate plots within the same age group ($p > 0.05$). Therefore, all nutrient dynamics analyses were done by pooling the data of replicate plots of an age group.

Allometric relationship linear regression equations ($Y = a + bX$, where Y and X are nutrient content and girth, respectively, and a and b are the constants) were developed for each age group using girth at breast height (in the case of one year old plantation girth measuring height was chosen 50 cm above ground level) as the independent variable and total tree, above ground and below ground N and P storage as dependent variables. Equations were also developed for all the age classes together by pooling the data for all trees belonging to all plantations. Regression analysis was also done to establish relationship between age and nutrient stored in various compartments such as bole wood (bark + bole), crown wood (branch + twigs), foliage (leaves), roots (stump root + lateral roots) and seeds.

Results and Discussion

Nutrient content

Content patterns for N and P and the N: P ratio varied in different plant parts (Table 1). Content percentage of N was recorded in the following order: foliage > seed > lateral root > fine root > stump root > bark > twig > bole = branch. P content decreased in the following order: lateral root > seed > stump root > foliage > bole > bark > twig = fine root > branch. N: P ratio was in the order as follows: foliage > fine root > seed > bark > twig > branch > lateral root > stump root > bole.

Table 1. Nutrient content ($\mu g \cdot g^{-1}$) and N : P ratio in different tree components of young teak plantations (mean ± se)

Components	N	P	N:P
Bark	6000 (±200)	1100 (±100)	5.45
Bole	3100 (±200)	1500 (±60)	2.06
Branch	3100 (±100)	700 (±80)	4.42
Twig	5300 (±400)	1000 (±50)	5.30
Leaf	15100 (±100)	1600 (±50)	9.43
Seed	13300 (±400)	2200 (±90)	6.04
Stump root	6400 (±100)	2100 (±100)	3.04
Lateral root	7600 (±300)	2400 (±200)	3.16
Fine root	7500 (±100)	1000 (±60)	7.50

Foliage had the highest N content while roots had the highest P content. These results are in partial agreement with George and Verghese (1992) reporting on a 20-year old teak plantation whose leaves possessed the highest content of all nutrients followed by root, branch, bark and wood. Many other workers reported that leaves, being the most metabolically active part of the tree, contained the highest concentrations of nutrients (Bargali et al. 1992; Chen 1998; Deans et al. 1999; Harrison et al. 2000;

Ingerslev 1999; Li 1996; Lodhiyal et al. 1995; Peri et al. 2006; Rawat and Tandon 1993; Regina 2000; Singh and Singh 1991; Subramanian et al. 2009; Thakur and Swamy 2010; Wang et al. 1995and 1996). However, Mishra et al. (1998) reported similar results regarding higher content of P in roots compared with leaves and other other parts of the tree. Contents of N (15,100 $\mu g \cdot g^{-1}$) and P (1600 $\mu g \cdot g^{-1}$) in foliage are comparable to the findings of George and Verghese (1992), that N is 16,000 $\mu g \cdot g^{-1}$ and P is 1,100 $\mu g \ g^{-1}$. Faruqui (1972), reporting on teak in a climate similar to that of our study documented very high nutrient concentrations (N, 25,000 to 27,500 $\mu g \cdot g^{-1}$ and P, 2,700 to 4200 $\mu g \cdot g^{-1}$) compared with these two findings. Kumar et al. (2009) studied teak but in a drier region and reported higher nutrient content (26,800 $\mu g \cdot g^{-1}$ N and 2,100 $\mu g \cdot g^{-1}$ P). Substantial variation in the concentration of these two nutrients in different plant parts might be due to wide variation in climatic factors. It is also possible that genetic makeup of the trees could have played its role. Wu et al. (2006) concluded that the mineral nutrient status of the plant is controlled by its genetically fixed nutrient uptake potential, nutrient availability in the soil, and the environmental factors of slope, elevation, topography and climate.

Our calculated range of nutrient concentration ratio (N : P) was low (2.06 to 9.43) compared to the report of Medina (1980) in tropical dry deciduous forests (12 to16). This might be attributed to the moist nature of the tropical deciduous forest where nutrient status in the soil is comparatively higher. Our foli-

age:wood nutrient content ratio (4.8 for N and 1.06 for P) is also low compared to temperate trees (16.6 for N and 10.3 for P; in Bargali 1990).   However, comparison of our ratios with others for tropical trees (4.8 N and 2.7 P) showed that our N and P ratios were equal to (N) or similar to (P) the results of others. Thus, there is an indication that teak had similar nutrient accumulation pattern as the tropical trees.

Standing state

Range of total standing state in all the stands was 20.3−586.6 $kg \cdot ha^{-1}$ for N and 5.3−208.8 $kg \cdot ha^{-1}$ for P. Above ground and below ground nutrient storage ranges were 12.5−462.4 $kg \cdot ha^{-1}$ and 7.8−124.2 $kg \cdot ha^{-1}$, respectively for N, and 2.8−167.9 $kg \cdot ha^{-1}$ and 2.5−40 $kg \cdot ha^{-1}$, respectively for P. All minima and maxima in these ranges were from 1 to 30-year plantations. Review of nutrient storage data in different components of different aged stands indicated that storage of N and P increased in bark, bole, stump root and lateral root with increasing stand age. Above ground and below ground content also followed this pattern. But in the case of branch, twig and foliage, the relationship of nutrient storage with increasing stand age was non linear. Regression relation of bole wood, crown wood and roots with stand age were highly significant (p <0.01). However, the relationship between foliage and age was not significant (Fig. 2).
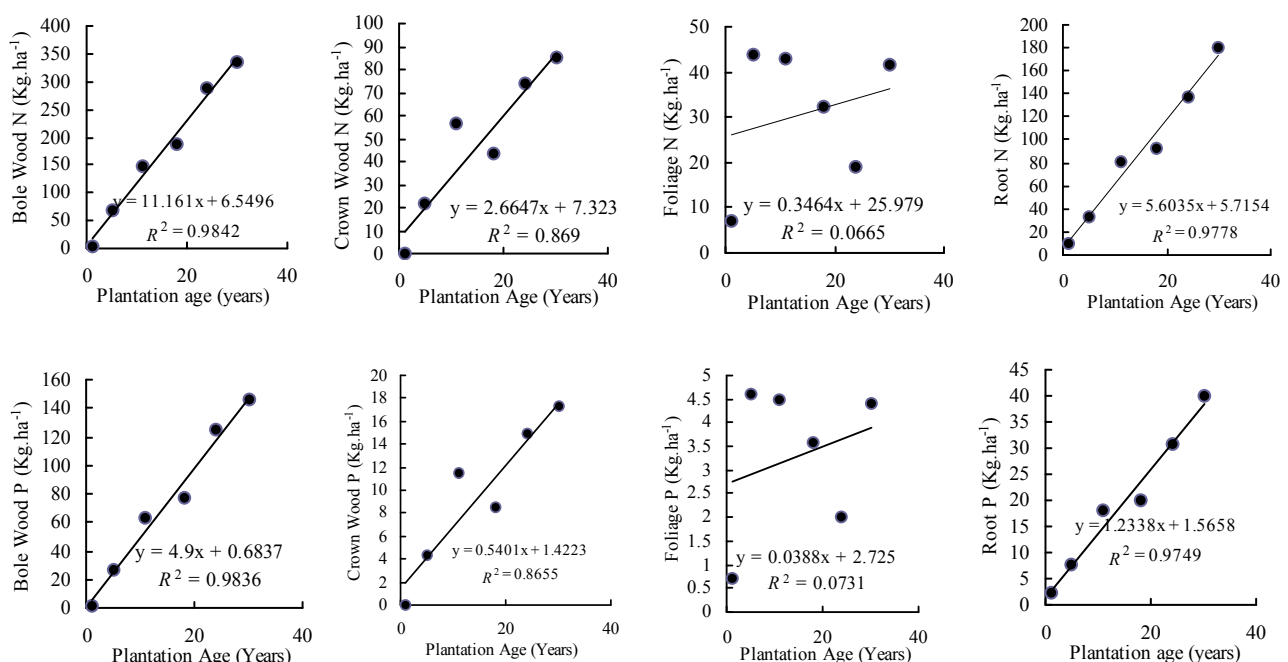

Fig. 2. Storage of nutrients (N and P) in different compartments of teak tree as affected by the age of the plantation. Linear regression relationship for both the nutrients were highly significant (p = 0.01) for bole wood (bark + bole), crown wood (branch + twigs) and roots (stump root + lateral roots), but it was not significant for foliage (p >0.05).

Average percentage of resource allocation in different plant parts such as bark, bole, branch, twig, foliage stump root, and lateral root for N were 10.5%, 44.6%, 6.7%, 11.3%, 10.0%,

11.1% and 8.6%, and for P, 5.6%, 63.4%, 4.4%, 6.2%, 3.1%, 10.7%, 8.0%, respectively. Above ground and below ground allocations were 80.2 and 19.8% for N and 81.1 and 18.7% for P.

Distribution of nutrients by tree component in different stands differed considerably on account of biomass variation. As the age of the crop (or biomass) increased total storage also increased linearly. Ovington (1959) reported similar results in forest crops and Bargali et al. (1992) and Harrison et al. (2000) in eucalyptus plantations. Bargali et al. (1992) differed, however, on account of maximum storage in a particular tree component. Leaves stored maximum nutrients in contrast to the present study where bole wood stored the most. Nonetheless, our results supported those of George and Verghese (1991) in *Eucalyptus globulus*, and George and Verghese (1992), and Adu-Anning and Blay (2001) in *Tectona grandis*. Thus, biomass plays a more important role in nutrient accumulation than nutrient concentration in different plant parts. Rawat and Tandon (1993) also observed that percent concentration of a particular nutrient for a particular component, in the case of *Pinus*, need not show consistent trend or relationship with age.

Average storage of N (312 kg·ha^{-1}) was comparable to the findings of Jordan et al. (1982) in tropical wet forests of Venezuela and Negi et al. (1995) in teak plantations on the *Tarai* (336 kg·ha^{-1} and 331 kg·ha^{-1}, respectively), and P (106 kg·ha^{-1}) to Golley et al. (1975) in tropical moist forests of Panama (114 kg·ha^{-1}). However, in dry deciduous forests of India (Pandey 1980; Singh and Singh 1991) N storage was much higher (717, 567), while P was much lower (56, 37). Further, in the same locality, N was lower in *Eucalyptus* hybrid (Bargali 1990) and higher in *Populus deltoides* (Lodhiyal et al. 1995) but P was lower in both of these findings. Thus, the nutrient storage depended at least on age, plant species and edaphoclimatic factors.

Retranslocation

The ranges of retranslocated amounts for N and P were 8.7 to 48.0 kg·ha^{-1}·a^{-1} and 0.1 to 3.5 kg·ha^{-1}·a^{-1}, respectively. Similarly, percent retranslocation range for N was 32.3 to 59.9% with minimum values in the one year and maximum in the 11 year old plantations. For P this range was 3.7 to 43.5%, and minimum values were for the one year and maximum for the 18-year-old plantation. The regression relationship between age and nutrient retranslocation was significant at 5% for N but it was not significant for P (Fig. 3).

Average nutrient retranslocation was moderate (45.3% N and 27.5% P), indicating a substantial role for nutrient uptake and a nutrient-rich system as suggested by Chapin (1980) and Singh et al. (1984) that retranslocation is more effective in nutrient poor systems where the tree withdrawal was high. Although, relationship between retranslocation percent and age of stands was found positive by Chapin and Kedrowski (1983) and negative by few other workers (Bargali 1990; Lodhiyal et al. 1995; Ralhan and Singh 1987), the present study did not find a clear linear relationship between age and retranslocation percent. Both N and P retranslocation increased up to 18 years and then decreased until 30 years. The reason could be the influence of more than one factor on retranslocation, such as growth forms, climate and ecophysiology as suggested by Ralhan and Singh (1987) and Fife and Nambiar (1997).
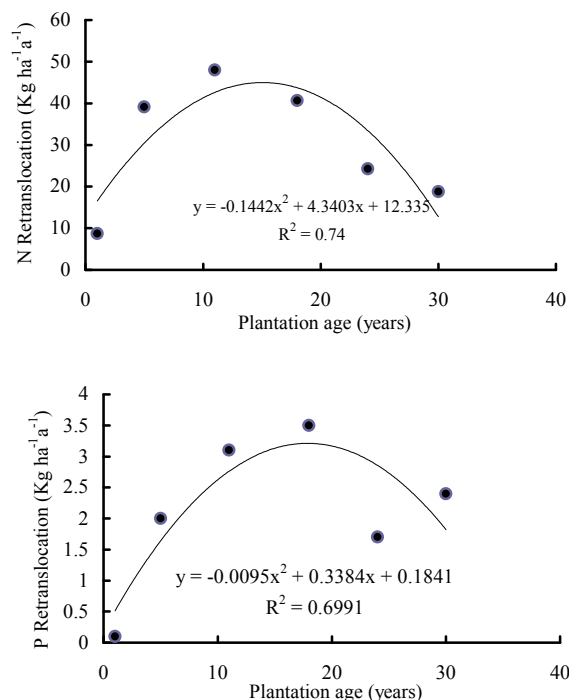

Fig. 3. Influence of plantation age on the foliar retranslocation of nutrients (N and P) in teak. The relationship was significant for both the nutrients (p <0.005) in polynomial regression.

Nutrient uptake

The nutrient uptake range of N was from 28.2 to 125.2 kg·ha^{-1}·a^{-1} and for P from 3.3 to 20.2 kg·ha^{-1}·a^{-1} (Table 2). In both cases, the highest uptake was in five year and the lowest in one year old plantation. Gross uptake analysis by plant component indicated that leaves partitioned maximum uptake of nutrients followed by bole while roots partitioned minimum nutrients, except in one year old plantation where N content in roots was more than in boles.

Distribution percentage of average gross uptake by age in different plant parts like bark, bole, branch, twig, foliage, fruit, stump root and lateral root were 2.1%, 7.9%, 1.4%, 5.5%, 78.7%, 1.7%, 2.1% and 2.1% for N, respectively, and 2.6%, 25.2%, 2.0%, 6.7%, 54.5%, 1.8%, 4.5% and 4.4% for P, respectively. Above ground and below ground allocations were 95.8% and 4.2% for N and 91.0% and 8.9% for P.

Amount of net uptake (after correction for retranslocation) in different plantations for N ranged from 19.4 to 88.9 kg·ha^{-1}·a^{-1} and P from 3.8 to 18.1 kg·ha^{-1}·a^{-1}. Minimum and maximum uptake for N was in one and 30-year old plantations, respectively. For P one-year old plantation had minimum uptake but maximum uptake was in five-year old plantation. Uptake patterns of these two nutrients among different plant parts were also not consistent. However, overall N uptake was always higher than P.

Rodin and Bazilevich (1967) reported that the amount of nutrient uptake is, generally, directly proportional to net primary production. The total amount of uptake (88.1 kg·ha^{-1}·a^{-1} for N and 13.5 kg·ha^{-1}·a^{-1} for P) in the present study fell within the

range recorded in literature (87 to 256 kg·ha^{-1}·a^{-1} N and 4 to 134 kg·ha^{-1}·a^{-1} P) . However, N value was closer to mixed broad leaf forest of Japan (Iwatsubo 1976) and P value to oak forest of India (Rawat and Singh 1988).

Table 2. N and P uptake (kg·ha^{-1}·a^{-1}) in teak plantations at different age

Tree parts	N						P					
	1 year	5 years	11 years	18 years	24 years	30 years	1 year	5 years	11 years	18 years	24 years	30 years
Bark	0.90	4.57	1.68	1.86	0.94	1.21	0.20	0.84	0.30	0.34	0.17	0.22
Bole	0.52	12.1	8.36	8.65	5.57	6.69	0.25	5.86	4.05	4.18	2.69	3.37
Branch	0	1.87	1.47	0.86	0.55	1.43	0	0.42	0.33	0.19	0.12	0.32
Twig	0	4.48	5.55	5.20	4.17	4.62	0	0.85	1.05	0.98	0.79	0.87
Leaf	26.9	95.2	80.1	77.7	49.9	86.4	2.85	10.1	8.48	8.23	5.29	9.15
Fruit	0	0.58	1.35	2.54	0.35	2.60	0	0.09	0.22	0.42	0.06	0.43
Aboveground	27.5	119	98.5	96.8	61.6	103	3.12	18.1	14.4	14.3	9.13	14.4
Stump root	0.39	3.34	2.25	2.20	0.85	2.12	0.13	1.09	0.73	0.72	0.28	0.69
Lateral root	0.20	2.98	1.94	2.72	1.06	2.34	0.06	0.94	0.61	0.86	0.33	0.74
Belowground	0.59	6.32	4.19	4.92	1.92	4.47	0.19	2.04	1.35	1.58	0.61	1.44
Total	28.1	125	102	102	63.5	108	3.32	20.2	15.8	15.9	9.7	15.8

Net N uptake in 30 year old teak plantation (89 Iwatsubo) was quite low compared to the other systems of the region of the present study such as natural Sal forest (125 Iwatsubo), Himalayan oak forest (91 to 148 kg·ha^{-1}·a^{-1}) and poplar plantation (124 kg·ha^{-1}·a^{-1}). However, P uptake at 30 years (13.32 kg·ha^{-1}·a^{-1}) was higher than Sal (8 kg·ha^{-1}·a^{-1}), Himalayan oak forest (10 kg·ha^{-1}·year^{-1}) and Eucalypt (10 kg·ha^{-1}·a^{-1}).

Highest nutrient uptake in five year old plantation indicated that nutrient requirement at this stage was more for structure building than in the other age classes. This may be due to the fact that at initial age teak grows faster than many other timber species. Maximum nutrient need in foliage is related to the highest biological activity in leaf compared to the other ground parts. Further, lowest nutrient need in roots suggested that nutrient requirement was lowest for structural building. This corroborated the fact that root development was very slow compared to above ground parts.

Nutrient return

Return of the nutrients was highest from the foliage followed by the twigs and the fruits. The range of total return across the stands was 25.8 to 91.3 kg·ha^{-1}·a^{-1} for N and 2.7 to 10.1 kg·ha^{-1}·a^{-1} for P and the average return for all the stands was 70.5 kg·ha^{-1}·a^{-1} N and 7.7 kg·ha^{-1}·a^{-1} P. Distribution percentage of annual shedding of these resources in different forms of leaf litter, twig litter and reproductive parts were 94.9%, 4.0% and 2.1%, respectively for N and 91.6%, 6.8% and 3.2%, respectively for P.

Average annual return in the present study (70.4 kg·ha^{-1}·a^{-1} N and 7.7 kg·ha^{-1}·a^{-1} P) fell well within the reported range of 64 to 162 kg·ha^{-1}·a^{-1} and 2.6 to 8.8 kg·ha^{-1}·a^{-1}, respectively for N and P in moist tropical forests (Vitousek and Sanford 1986). Our results approximated findings in the same locality by Lodhiyal (1990) in *Populus deltoides*, Bargali (1990) in *Eucalyptus* hybrid and Lodhiyal et al. (2002) in *Dalbergia sissoo* at shorter rotation. Although this may not hold true for all regions, there was an indication that in the Himalayan *Tarai* nutrient return, at least for

N and P, is almost similar in introduced species such as eucalyptus, poplar and teak.

Nutrient use efficiency

Nutrient use efficiency (ratio of annual net productivity to nutrient uptake by weight (Hirose 1975)) for N (NUE) and P (PUE) between one and 30 years varied in an inconsistent pattern (Table 3). NUE increased from 1 to 11 years and then decreased till 30 years. PUE increased from one to 18 years and then decreased. Highest and lowest NUE and PUE were 107.4 and 192.5 g OM·g^{-1}, and 551.9 and 841.1 g OM·g^{-1}, respectively. However, PUE was 4.3 to 6.7 times higher than NUE.

Table 3. Nutrient Use Efficiency of young teak plantations

Age (year)	N		P		PUE/NUE
	Net uptake (kg·ha^{-1})	NUE (g OM·g^{-1})	Net uptake (kg·ha^{-1})	PUE (g OM·g^{-1})	
1	19.42	107.4	3.78	551.9	5.1
5	86.05	155.6	18.09	740.4	4.8
11	54.65	192.5	12.63	832.9	4.3
18	61	170.7	12.38	841.1	4.9
24	39.15	167.0	7.97	820.5	4.9
30	88.89	116.5	13.32	777.3	6.7

Nutrient use efficiency provides a good measure to evaluate large differences in nutrient "costs" of biomass production (Wang et al. 1991). Sharma (1993) in a monoculture of Himalyan alder and Sharma et al. (2002) in the mixed plantation of *Alnus-cardamom* hypothesized that nutrient use efficiency for both N and P decreased with age, which was not true in the present study. Initially nutrient use efficiency increased up to 11 and 18 years and then declined until 30 years. This may be due to factors other than age alone that control nutrient use efficiency. However, Kumar et al. (1998) suggested that it was a function of the cultural system and age of the crop independently or in combination. NUE at the age of 30 years in teak was higher than at

the same age of a high altitude *Alnus* mixed plantation but PUE was less than half. It was also hypothesized that nutrient use efficiency helps explain species distribution across landscapes that vary in soil fertility (Rundel 1982; Vitousek 1982; Schlesinger et al. 1989). NUE (95–150 g OM·g^{-1} N) and PUE (433–962 g OM·g^{-1} P) reported by Hiremath et al. (2002) in three tropical fast growing species (*Hyeronima alchorneoides*, *Cedrela odorata* and *Cordia alliodora*) was lower than the present study. This may be due to the difference in site characters of the two study sites. The former is a very high rainfall zone with 25°C annual mean temperature and soil is rich in N and P contents. This is supported by the hypothesis of Hiremath et al. (2002) that low nutrient use efficiency reflected high soil fertility.

Nutrient turnover time

The turnover time of N and P, calculated on the basis of standing state of nutrients, varied between 2.0 and 2.4 years, respectively in one year-old plantation and 13.2 and 22.7 years, respectively in 24 year-old plantation. Although turnover tended to increase with age, the relationship was inconsistent within the intermediate age group plantations. Turnover time for P was 1.2 to 2.2 times higher than for N. However, regression showed that the relationship between age and turnover time of nutrients was significant at 5% level (Fig. 4).
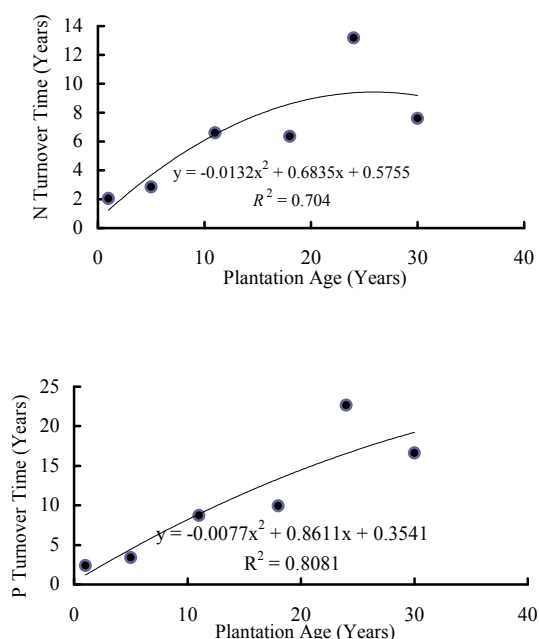

Fig. 4. Turn over time of nutrients (N and P) in teak plantation of different age group. The relationship was significant for both the nutrients ($p < 0.005$) in polynomial regression.

Turnover time of nutrients in standing vegetation reflects the rate of nutrient cycling. Sharma et al (2002) reported in *Alnus nepalensis* that turnover times of N and P, though have an inconsistent relationship with age and showed an increasing trend.

Findings of the present study were consistent with this report. However, turnover time was higher in the present study as compared to their report. This may be due to the fact that estimates of turnover rates require steady state conditions, which are not met in growing plantations. Also the contrary is the relationship between turnover times of these two nutrients. They recorded that turnover time of P was lower than N while our study suggested the opposite relationship.

Soil nutrients

Nitrogen concentrations in soil ranged from 690 to 1,210 µg·g^{-1} and P concentration ranged from 100 to 140 µg·g^{-1} dry soil (Table 4). Nutrient content percent and total storage of nutrient in 30 cm deep soil varied with stand age but the relationship between both was inconsistent. This finding was not inconsistent with Bargali (1990) in eucalyptus and Lodhiyal (1990) in poplar plantations grown in the same locality. However, total storage in the soil pool decreased from the one year-old plantation (3,496.8 N, 446.4 P) to the 30 year-old plantation (3,087.6 N, 372 P). In 24 year-old plantation, these components (2,566.8 N, 372 P) were still lower. This may be attributed to the fact that, from the soil properties point of view, this plantation was much older than 30 years because this crop was the second rotation of teak (24 years of second rotation and 50 years of first rotation).

Table 4. Nutrient content (µg·g^{-1}) in the soil of teak plantations (mean±se)

Age	Nutrient content	
(year)	N	P
1	940 (±240)	120 (±50)
5	1190 (±290)	140 (±100)
11	940 (±380)	110 (±90)
18	1210 (±440)	120 (±100)
24	690 (±550)	100 (±180)
30	830 (±210)	100 (±60)

Allometric relationship

Twenty-one equations for N and P storage in tree, above ground and below ground vegetation in all the age groups and across the age groups together are listed in Table 5. Only three equations for both nutrients in one year-old plantation were not significant. The remaining thirty-six equations were significant at 1% level. These relationships indicate that these equations can be used to estimae nutrient accumulation in teak trees growing in similar conditions.

Nutrient cycling

As suggested by Singh et al. (1979), an ecological system may be visualized as a set of compartments interconnected by flow of dry matter, energy and information. The selection of a set of compartments to be used in a particular situation is usually made on the basis of existing knowledge of structure and function relationship among the morphologically, physiologically, or con-

ceptually recognizable "sub units" of the system. In teak plantation ecosystems, vegetal structure virtually consists of trees only since herbs and shrubs do not contribute significantly to productivity (Jha 1995). The tree components have been divided into a set of three compartments, *viz.* leaves, wood and root. Litter and soil compartments are also the part of the system. Compartment models of nutrient dynamics (N and P) are depicted in Fig. 5 and

Fig. 6. Mean standing states are given in pools, annual flux on arrows and retranslocation (internal cycling) on solid arrows. In these figures direction of nutrient flux - from soil to foliage indicated a one way movement, although nutrients utilized by foliage in organic matter synthesis were redistributed among different components during the assimilate transfers (Singh and Singh 1991).

Table 5. Allometric relationship between girth and nutrient content in teak plantations

Age (year)	Components	Nitrogen			Phosphorus		
		Intercept	Slope	r^2	Intercept	Slope	r^2
1	Total	1.237	0.068	0.116ns	0.247	0.014	0.116ns
	Aboveground	-0.481	0.169	0.642ns	-0.096	0.034	0.642ns
	Belowground	1.718	-0.101	0.726ns	0.344	-0.020	0.642ns
5	Total	-13.942	1.083	0.862**	-2.788	0.217	0.852**
	Aboveground	-12.362	0.957	0.862**	-2.472	0.191	0.862**
	Belowground	-1.580	0.126	0.745**	-0.316	0.025	0.745**
11	Total	-205.270	5.549	0.961**	-41.054	1.110	0.961**
	Aboveground	-181.772	4.898	0.959**	-36.354	0.980	0.959**
	Belowground	-23.498	0.651	0.919**	-4.700	0.130	0.919**
18	Total	-177.872	4.994	0.940**	-35.574	0.999	0.940**
	Aboveground	-149.522	4.271	0.951**	-29.904	0.854	0.951**
	Belowground	-28.350	0.724	0.802**	-5.670	0.145	0.802**
24	Total	-248.851	6.583	0.942**	-49.770	1.317	0.942**
	Aboveground	-229.788	5.928	0.941**	-45.958	1.186	0.941**
	Belowground	-19.062	0.655	0.921**	-3.812	0.131	0.921**
30	Total	-377.442	7.978	0.940**	-75.488	1.596	0.940**
	Aboveground	-312.872	6.763	0.931**	-62.574	1.353	0.931**
	Belowground	-64.570	1.216	0.748**	-12.914	0.243	0.748**
1−30	Total	-192.021	5.935	0.903**	-38.404	1.187	0.903**
	Aboveground	-165.554	5.146	0.903**	-33.111	1.029	0.903**
	Belowground	-26.467	0.789	0.781**	-5.293	0.158	0.781**

ns: not significant, **: significant at 1%

Total quantity of nutrient stored in vegetation (standing state of nutrients) increased with age from 20.3 kg·ha^{-1} N and 5.3 kg·ha^{-1} P to 586.6 kg·ha^{-1} N and 208 kg·ha^{-1} P in one-year to 30-year old plantations, respectively. Out of these total quantities above ground storage was 12.5 kg·ha^{-1} N, and 2.8 kg·ha^{-1} P in one year-old stands while 462.4 kg·ha^{-1} N, and 167.9 kg·ha^{-1} P in 30 year-old stands. The below ground quantity was 7.8 kg·ha^{-1} N, and 2.5 kg·ha^{-1} P at one year while 124.2 kg·ha^{-1} N, and 40 kg·ha^{-1} P in 30 year-old plantations.

Higher nutrient storage in soil in one year-old plantation than in 30 year-old plantation indicated that during the course of teak growth soil nutrients were depleted. This was due to less annual return of nutrient to soil during the considered span than the annual uptake. This type of cycling pattern was reported for eucalypts on *Tarai* soil (Jha and Chhimwal 1993) and on lateritic soil (Nandi et al. 1991). Boreman and Likens (1979) suggested that degradation of soil was likely to happen in all plantations that replaced natural forests after clear cutting as was done in the area of the present study.

However, annual nutrient input to the soil from decomposing litter varied between minima of 17.0 N and 1.8 P (one year) and

maxima of 60.3 N, 6.6 P (30 years). Though decomposition of fine roots also contributed to soil nutrient content, values of annual uptake were much higher (70.2 N, 22.5 P for one year; 1117.8 N, 360 P for 30 years; which increased with age). Although the ecosystem function is very complex, this gap between uptake and supply of nutrients may be one of the explanations for depleting soil nutrients. However, Subramanian et al. (2009) surprisingly suggested that as the age of a plantation increases, teak becomes an eco-friendly species by not affecting the ecology of the site, since it retains more nutrient than it returns as the plantation ages.

When the total system was taken into account, average distribution of N and P in tree, litter, and soil was 8.4% and 19.1%, 1.8% and 1.4%, and 89.8% and 79.4%, respectively. However, percentage contribution of N in soil decreased from 99% to 82% while it increased in the tree layer from 0.5% to 15.6% with increasing age. Phosphorus showed the same trend, decreasing from 98.5% to 63% in soil and increasing from 1% to 35% in the tree layer with age. Percentage contribution of these two nutrients in litter showed inconsistent relationships with age.
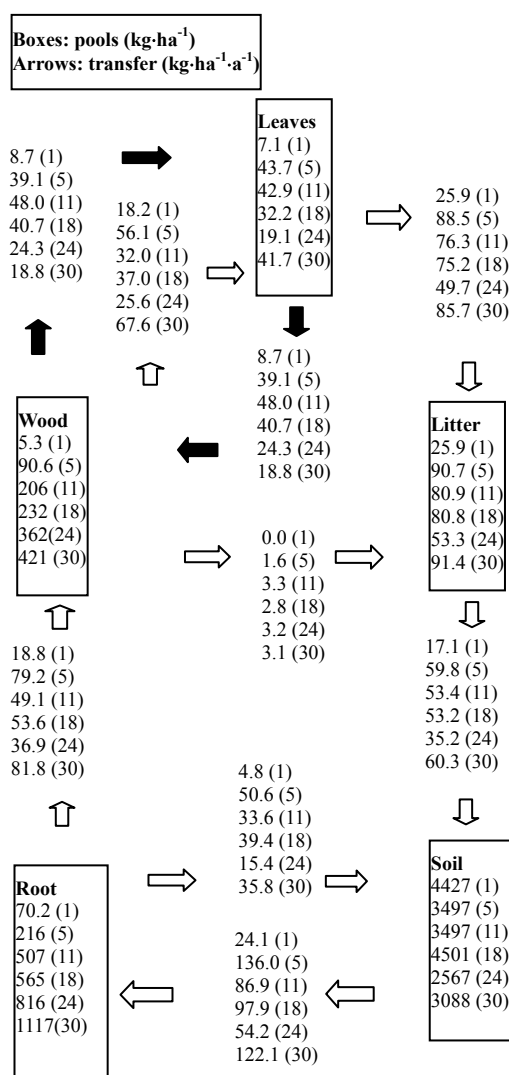
Fig. 5. A compartment model showing annual N budget for different age plantations (age in brackets against each value). Arrows show one-way movement. Values in boxes represent N content (kg·ha⁻¹). Net annual fluxes (kg·ha⁻¹·a⁻¹) are presented on arrows between the compartments. Dark arrows give the magnitude of N (kg·ha⁻¹·a⁻¹) associated with retranslocation.

Fig. 6. A compartment model showing annual P budget for different age plantations (age in brackets against each value). Arrows show one-way movement. Values in boxes represent P content (kg·ha⁻¹). Net annual fluxes (kg·ha⁻¹·a⁻¹) are presented on arrows between the compartments. Dark arrows give the magnitude of P (kg·ha⁻¹·a⁻¹) associated with retranslocation.

Ranger and Colin-Belgrand (1996) reported that decreasing rotation length will enhance the depletion of forest soil nutrients, as will harvesting a larger part of the forest biomass compartments, which contain most of the nutrient in the vegetation. Findings in our study were contrary. If rotation is reduced below 30 years, nutrient removal will be lowered since its accumulation in trees was lower at younger age.

Harvest loss

Several tropical countries, including India, recently started growing teak on shorter rotations (Jha and Singh 1999). In short rotation, high yield plantation systems, nutrient accumulation
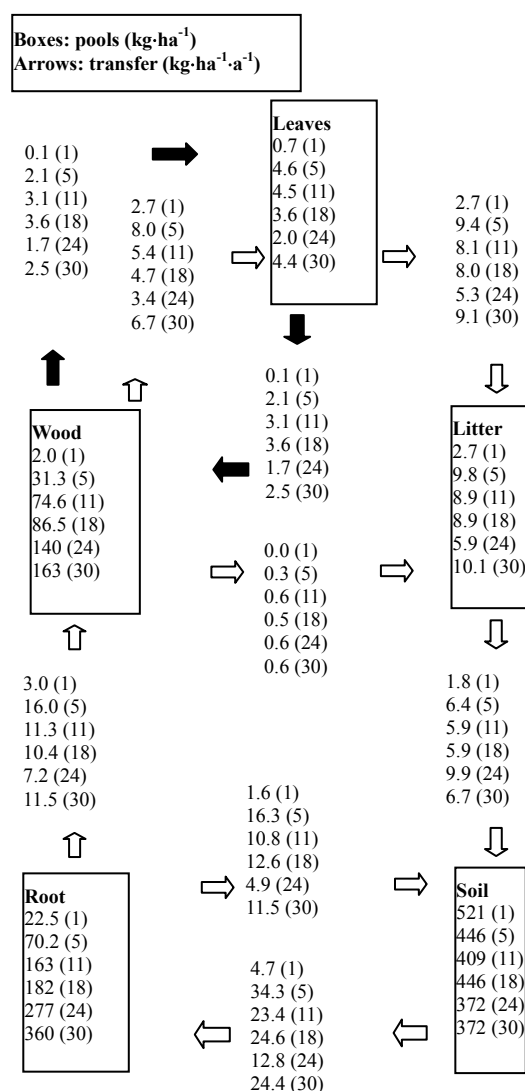
and export from the site have become important considerations (Hopman et al. 1993) because nutrients removed through frequent harvest may exceed the natural rate of input (Kumar et al. 1998). Harvesting of trees at any age represents the removal of the standing state (nutrients present in utilizable biomass) of the crop. Above ground removals of N and P at the age of 30 years in "whole tree harvesting" were 462.4 and 167.9 kg·ha⁻¹, respectively, while below ground removal in the case of "complete tree harvesting", due to uprooting of crop required for intercropping, was an additional 124.2 (N) and 40.0 (P) kg·ha⁻¹. In comparison with our results, assessment of above ground loss by Negi et al. (1995) in *Tarai* teak seem to be on the lower side (247 kg·ha⁻¹ N and 41 kg·ha⁻¹ P).

Monocultures have lower nutrient content compared to polycultures (Mishra 2011). Furthermore, possible impoverishment of soil as a result of harvesting cannot be ruled out in teak plantations. Kimmins (1997) also concluded that short rotation forestry combined with intensive biomass utilization created problems of reduced fertility. More specifically, Hase and Foelster (1983) reported that N and P stores were severely affected by introduction of teak afforestation. We recommend, therefore, that repeated cycles of teak must be interrupted with nutrient enriching broadleaved species (Wang et al. 2008) and mixtures of tree species (Awotoye et al. 2011), preferably indigenous species. Where possible, natural forest should not be converted into a monoculture of nutrient depleting species so that the edaphic balance of the area is maintained. We also suggest that only commercial biomass be removed from the site to minimize the nutrient drain: leaves, twigs and lateral roots must be left on site to restrain nutrient export.

Conclusion

We conclude the following in relation to the functioning of teak plantations: (1) Contents of nutrients (N, P) and N : P ratios inconsistent patterns amongst different plant parts of different age plantations; (2) Our foliage: wood nutrient content ratios indicate that accumulation patterns are similar to those of other tropical tree species; (3) Nutrient standing state increases consistently with age of the plantations; (4) Gross and net nutrient uptake, nutrient return and nutrient turnover time are inconsistent with age of plantations; (5) Nutrient return and gross uptake ratios indicate that in all studied plantations, annual N and P return exceeds uptake; (6) The nutrient conservation mechanism at different ages is efficient but the retranslocation pattern with increasing age is not consistent; (7) Quantity of soil nutrients is not consistent with age, but their contribution percentage to the system decreases with increasing age; (8) Tree girth at breast height was strongly related to nutrient storage.

These conclusions can help develop management interventions such as artificial as well as natural nutrient enrichment of soil if the species is to be harvested repeatedly on shorter rotations. These can also help in opting for alternate cropping system in the region.

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